

## CLADISTIC AND BIOGEOGRAPHIC ANALYSES OF *APSIL* MALLOCH AND *REYNOLDSIA* MALLOCH (DIPTERA: MUSCIDAE) OF SOUTHERN SOUTH AMERICA

CLAUDIO JOSÉ BARROS DE CARVALHO AND MÁRCIA SOUTO COURI

(CJBC) Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, 81531-990, Brazil (e-mail: cjbcbarva@bio.ufpr.br); (MSC) Departamento de Entomologia, Museu Nacional, Quinta da Boa Vista, 20940-040, Rio de Janeiro, RJ, Brazil (e-mail: mcouri@attglobal.net)

**Abstract.**—*Apsil* Malloch and *Reynoldsia* Malloch are genera endemic to Patagonia and southern Chile. A cladistic analysis for each genus is presented. The analysis of *Apsil* supports its monophyly on the basis of two synapomorphies, flat head and high gena. The phylogenetic relationships of *Apsil* species found are: ((*A. pennata* (*A. dilata*, *A. spatulata*)) ((*A. maculiventris*, *A. apicata*) (*A. maculipennis*, *A. biseta*)) *A. atripes*)). The analysis of *Reynoldsia* supports its monophyly on the basis of very long and slender palpi. The phylogenetic relationships of *Reynoldsia* species found are: ((*R. pectinata* (*R. pteropleuraris*, *R. rufoapicata*)) (*R. coxata* (*R. brevitarsis* (*R. aurifera*, *R. scutellata*))))). The cladistic biogeographic analysis of both genera shows a distribution pattern congruent with recent biogeographic reconstructions of southern South America. The distribution pattern of *Apsil* species is more restricted than that of *Reynoldsia*. By the distribution pattern found in *Reynoldsia*, the occurrence of *Reynoldsia* species on Malvinas Islands could be expected.

**Key Words:** *Apsil*, *Reynoldsia*, Muscidae, cladistic, biogeography, South America

Among the 29 recognized genera of the Coenosiini (Muscidae, Coenosiinae) (Couri and Pont 2000), *Apsil* and *Reynoldsia*, both described by Malloch (1929, 1934), are the only ones endemic to Patagonia and southern Chile. Both genera can be easily recognized with the key to the world genera of the Coenosiini (Couri and Pont 1999).

According to Hennig (1959), the cosmopolitan range of many genera is regarded as indicator of their antiquity. Skidmore (1985) called attention to the predominance of the coenosines over other muscids both in polar regions and in the high montane equatorial regions.

All known adults of Coenosiinae are predators and are possibly so also in the

larval stage. No second instar coenosiine larva has been described (except for certain *Lispe*) and probably they are all monomorphic (Skidmore 1985).

Few references to these taxa have been made in the literature since the original descriptions. Recently, Couri (1995, 1998) re-described *Reynoldsia* and Couri (2000) revised the eight known *Apsil* species.

Our objectives are to perform a cladistic analysis of the species of *Apsil* and *Reynoldsia* and to analyze the geographic distribution patterns of the species of these genera.

### MATERIAL AND METHODS

The cladistic analyses of *Apsil* and *Reynoldsia*, considered by Couri and Pont

Table 1. Data matrix and characters of the species of *Apsil* used in the analysis. 0 = plesiomorphic character states; 1 and 2 = apomorphic character states.

Outgroup	00000 00000 00000 00000 00
<i>A. pennata</i>	10011 00000 01000 01010 20
<i>A. dilata</i>	11111 00100 01010 00210 20
<i>A. spatulata</i>	11000 00000 01010 11210 12
<i>A. maculiventris</i>	11110 10120 01111 01001 21
<i>A. apicata</i>	11002 11010 01111 11011 02
<i>A. maculipeennis</i>	11010 10001 10101 10100 01
<i>A. biseta</i>	11011 10001 11111 10100 01
<i>A. atripes</i>	10111 11010 00011 10000 11

1. Shape of head. [0] round, not flat; [1] flat [ci:100; ri:100; weight:10; steps:1].
2. Male: color of the pollinosity at face. [0] silver; [1] golden [ci:50; ri:50; weight:2; steps:2].
3. Shape of eyes. [0] not elongate; [1] elongate [C.I.: 33; ri:0; weight:0; steps:3].
4. Width of gena. [0] high; [1] very high [ci:33; ri:0; weight:0; steps:3].
5. Number of frontal setae. [0] 5; [1] 4; [2] 3 [ci:40; ri:0; weight:0; steps:5].
6. Hairs at arista. [0] almost absent; [1] short hairs present [ci:100; ri:100; weight:10; steps:1].
7. Length of antennal flagellum related to pedicel. [0] twice longer or more; [1] less than twice longer [ci:50; ri:0; weight:0; steps:2] (unordered).
8. Enlargement at apex of palpi. [0] absent; [1] present. [ci:50; ri:0; weight:0; steps:2].
9. Acrostichals presutural hairs. [0] developed; [1] not developed; [2] one cilia [ci:66; ri:50; weight:3; steps:3].
10. Brown cloud at stigma in wind. [0] absent; [1] present [ci:100; ri:100; weight:10; steps:1].
11. Small dark mark in first posterior cell almost below apex of second vein. [0] absent; [1] present [ci:100; ri:100; weight:10; steps:1].
12. Length of hind tarsus related to hind tibia. [0] much over  $\frac{2}{3}$  as long as tibia; [1] not over  $\frac{2}{3}$  as long as tibia [ci:33; ri:0; weight:0; steps:3].
13. Color of tibia. [0] brown; [1] yellow or yellowish [ci:100; ri:100; weight:10; steps:1].
14. Size of claws and pulvilli. [0] developed; [1] very reduced [ci:33; ri:0; weight:0; steps:3].
15. Width of frons at level of anterior ocellus. [0] about  $\frac{1}{3}$ ; [1] larger than  $\frac{1}{3}$  [ci:100; ri:100; weight:10; steps:1].
16. Antennal insertion. [0] not projected; [1] slightly projected [ci:33; ri:33; weight:1; steps:3].
17. Insertion of antenna relative to the transverse mid-line of head (head viewed from in front). [0] near; [1] a little far above. [ci:33; ri:33; weight:1; steps:3].
18. Length of lower calypter related to upper one. [0] twice longer; [1] almost the same size; [2] 1.5 times longer [ci:100; ri:100; weight:10; steps:2] (unordered).
19. Posteroventral series of bristles at fore femur related to posterodorsal series. [0] not stouter than those of posterodorsal series; [1] stouter [ci:50; ri:66; weight:3; steps:2].
20. Brown marks at abdominal tergites 1+2, 3 and

(2000) as sister-groups, were made separately and were carried out using Hennig86 version 1.5 (Farris 1988), and "Tree Gardner" version 2.2 (Ramos 1997), a program designed for running Hennig86 under Windows environment. Minimum-length trees were calculated using options "ie" associated with "successive weighting." The data matrix and the characters are shown in Tables 1 and 2.

Eight species of *Apsil* were analyzed using on 22 characters, and *Reynold sia* with its seven species was analyzed using 25 characters. Characters were polarized by the outgroup method (Watrous and Wheeler 1981, Maddison et al. 1984). The outgroups were represented by three species: *Schoenomyza armipes* Malloch 1934, *Notoschoenomyza costata* Snyder 1957 and *Spathiphyromyia guttipennis* Thomson 1869. These three genera compose, together with *Apsil*, *Reynold sia*, and *Schoenomyzina* Malloch 1934, a larger monophyletic group of Coenosiini, according to Couri and Pont (2000) mainly distributed in southern South America. Characters were coded as binary and multistate, the latter were considered as additive or nonadditive (characters 18 and 22 in *Apsil*, and 7 and 20 in *Reynold sia*), depending on the availability of information on contiguity of states in the outgroups. Cladograms were made using WINCLADA (Nixon 1999, version 0.9.9 beta).

Cladistic biogeographic methods (see Morrone and Crisci 1995 for review) were used to construct taxon-area cladograms from the different taxon cladograms. A comparison of the general area cladogram was made based in some published papers.

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4 abdomen. [0] two marks; [1] a unique large mark [ci:100; ri:100; weight:10; steps:1] (unordered).

21. Color of abdominal tergite 5. [0] all same color; [1] with 2 longitudinal brown marks; [2] with 2 round brown marks [ci:33; ri:20; weight:0; steps:6].

22. Marks at scutellum. [0] all same colour; [1] with 2 lateral brown lines reaching the apex; [2] with 2 lateral brown lines reaching the apex [ci:66; ri:66; weight:4; steps:3] (unordered).

Table 2. Data matrix and characters of the species of *Reynold sia* used in the analysis. 0 = plesiomorphic character states; 1 and 2 = apomorphic character states; ? = missing data.

Outgroup	00000 00000 00000 00000 00000
<i>R. pectinata</i>	10001 12111 00011 11100 011??
<i>R. pteropleuralis</i>	10111 10111 01100 01011 ??010
<i>R. rufoapicata</i>	10111 12111 00110 01111 01011
<i>R. coxata</i>	11100 00001 10100 00002 10101
<i>R. brevitarsis</i>	11100 00001 11200 00000 100??
<i>R. aurifera</i>	11100 01000 10200 01110 ???01
<i>R. scutellata</i>	11100 00000 10201 10010 ???01

1. Shape of palpi. [0] not very long and slender; [1] very long and slender. [ci:100; ri:100; weight:10; steps:1].
2. Setulae on fronto-orbital plate. [0] numerous; [1] few and weak [ci:100; ri:100; weight:10; steps:1].
3. Setulae on parafrontale. [0] numerous; [1] few and weak [ci:50; ri:0; weight:0; steps:2].
4. Length of antennal flagellum related to pedicel. [0] twice longer or less; [1] more than twice longer [ci:100; ri:100; weight:10; steps:1].
5. Antennal insertion. [0] not projected; [1] slightly projected [ci:100; ri:100; weight:10; steps:1].
6. Width of gena. [0] not very high; [1] very high [ci:100; ri:100; weight:10; steps:1].
7. Color of pruinosity at face. [0] grey; [1] golden [2] silver. [ci:66; ri:0; weight:0; steps:3] (unordered).
8. Color of frontal triangle. [0] dark, contrasting with the ground colour; [1] not contrasting with the ground colour [ci:100; ri:100; weight:10; steps:1].
9. Length of frontal triangle. [0] short; [1] long [ci:100; ri:100; weight:10; steps:1].
10. Marks at scutellum. [0] all same colour; [1] with 2 lateral brown lines reaching the apex. [ci:50; ri:50; weight:2; steps:2].
11. Color of knob: [0] totally brown; [1] yellow and brown. [ci:100; ri:100; weight:10; steps:1].
12. Acrostichals presutural hairs. [0] developed; [1] not developed [ci:50; ri:0; weight:0; steps:2].
13. Disc of katepisternum: [0] with many ground-setulae; [1] with few ground-setulae; [2] almost bare [ci:66; ri:66; weight:4; steps:3].
14. Number of humeral bristles. [0] 2 or 3; [1] more than 3 [ci:50; ri:0; weight:0; steps:2].
15. Number of setae on median third of anteroventral surface of hind tibia: [0] 2; [1] 3 [ci:50; ri:0; weight:0; steps:2].
16. Number of setae on median third of anterodorsal surface of hind tibia: [0] 2 or 3; [1] 4 [ci:50; ri:0; weight:0; steps:2].
17. Number of setae on median third of anterodorsal surface of mid tibia: [0] 2; [1] 3 [ci:50; ri:66; weight:3; steps:2].
18. Number of supramedian setae on posterior surface of mid tibia: [0] 1; [1] 2 [ci:33; ri:0; weight:0; steps:3].
19. Color of fore femur. [0] all same colour, dark brown; [1] dark brown, yellow at apex [ci:50; ri:66; weight:3; steps:2].

The distribution data of *Apsil* and *Reynold sia* were taken from Malloch (1929, 1934) and (Couri 1995, 1998, 2000) (Appendices 1, 2).

## RESULTS AND DISCUSSION

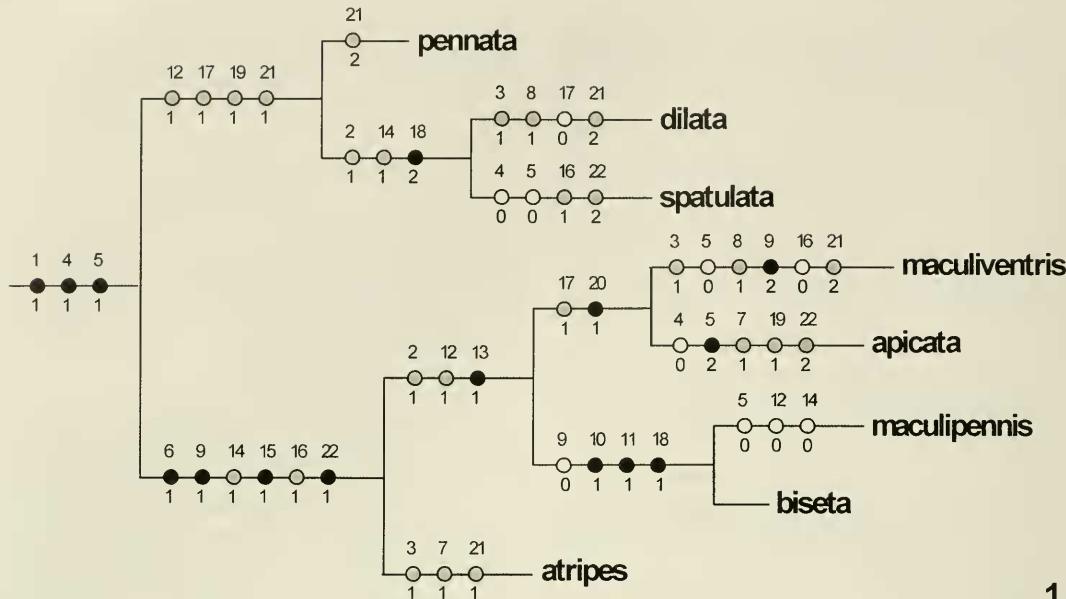
Phylogenetic analysis.—Only one tree was found for each analysis, with a length of 137 and 162, a consistency index (C.I.) of 88 and 91 and a retention index (R.I.) of 90 and 93, respectively for *Apsil* (Fig. 1) and *Reynold sia* (Fig. 2).

The analysis of *Apsil* supports its monophyly on the basis of the following shared synapomorphies: flat head, high gena and four frontal setae. The most basal dichotomy divides the genus into two groups: (*A. pennata* + *A. dilata* + *A. spatulata*) and (*A. maculiventris* + *A. apicata* + *A. maculipennis* + *A. biseta* + *A. atripes*), the latter defined by two synapomorphies; presence of short hairs at arista and width of the frons larger than  $\frac{1}{3}$  of head. *Apsil biseta* and *A. maculipennis* are the only *Apsil* species that show a brown cloud at the stigma in the wing, a small dark mark in the first posterior cell almost below the apex of the second vein, and the calypters almost of same size. Malloch (1934) mentioned the remarkable morphological similarity of these two species.

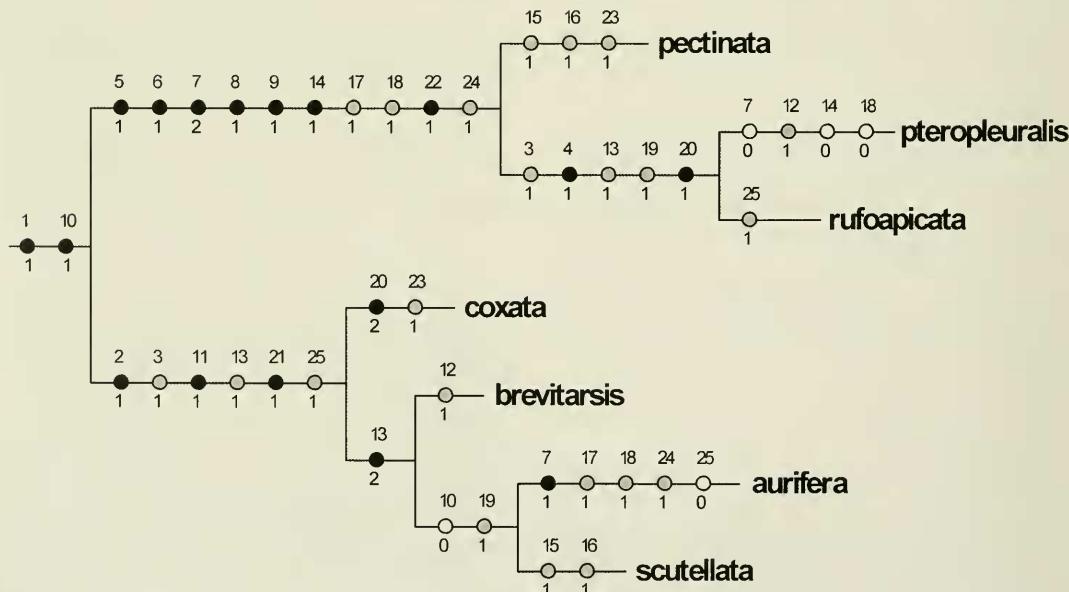
The analysis of *Reynold sia* supports its monophyly on the basis of very long and slender palpi. The most basal dichotomy di-

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20. Color of hind femur. [0] dark brown, yellow at apex; [1] dark brown on basal half and yellow at apical half; [2] totally dark brown [ci:100; ri:100; weight:10; steps:2] (unordered).
21. Sternite 5 arms. [0] large [1] medium [ci:100; ri:100; weight:10; steps:1].
22. Width of cercal plate. [0] large; [1] thin [ci:100; ri:100; weight:10; steps:1].
23. Aedeagus apodem. [0] shorter and larger; [1] longer and thinner [ci:50; ri:0; weight:0; steps:2].
24. Bristles on sternite 8 of ovipositor. [0] long and fine; [1] short and strong [ci:50; ri:50; weight:2; steps:2].
25. Shape of epiproct. [0] not divided; [1] divided [ci:33; ri:0; weight:0; steps:3].



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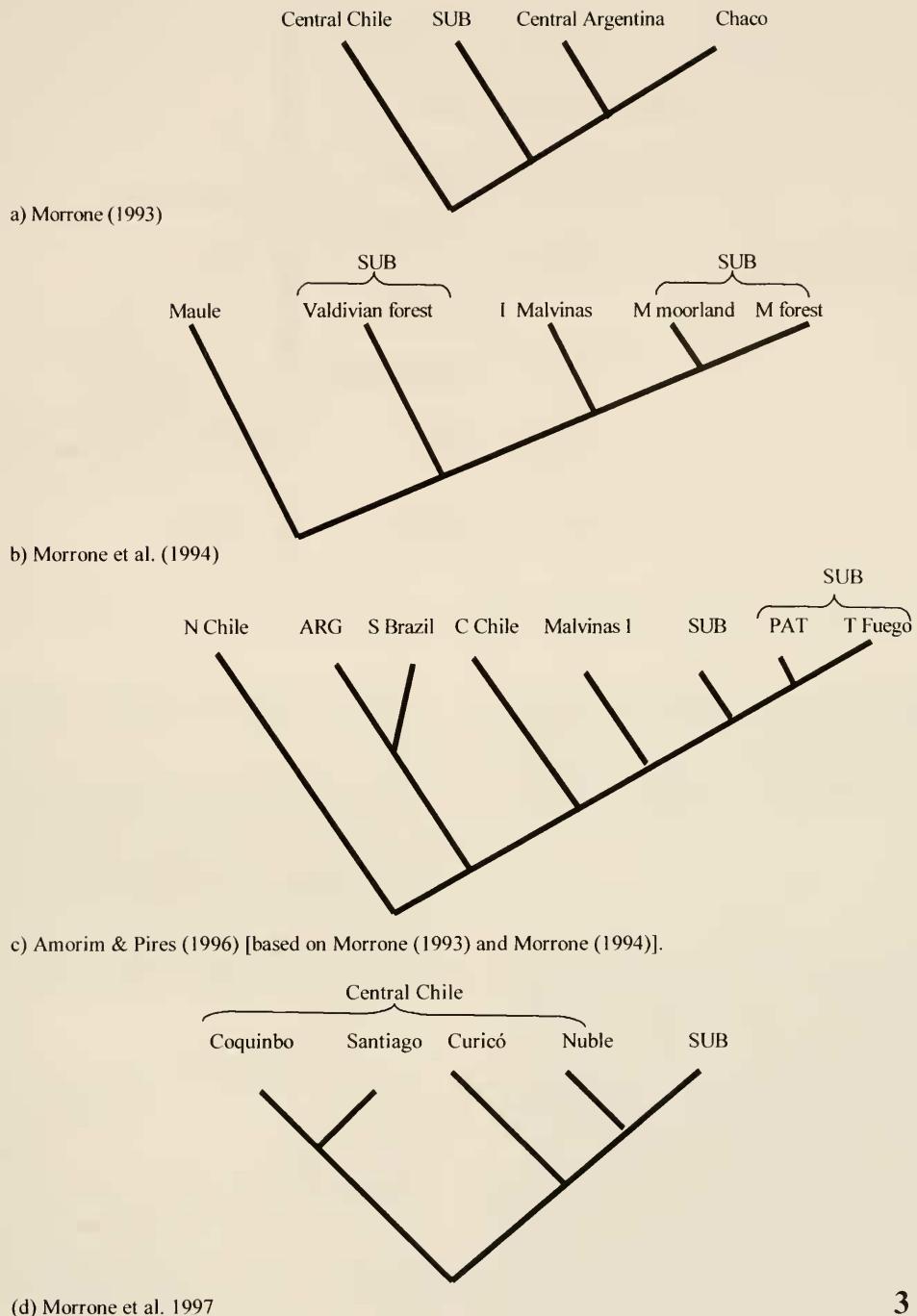


Fig. 3. Biological area cladogram for southern South America. C = Central; I = Isles; M = Magellanic; N = North; PAT = Patagonian province; S = South; SUB = Subantarctic province; T = Tierra del.

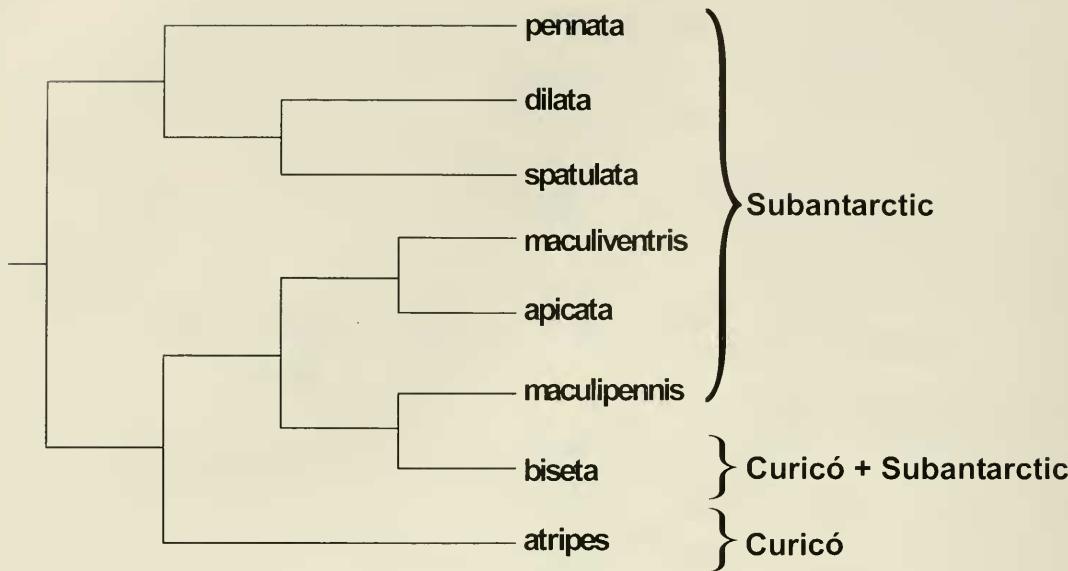


Fig. 4. Taxon-area cladogram of species of *Apsil*.

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vides the genus into two groups: (*R. pectinata* + *R. pteropleuralis* + *R. rufoapicata*) and (*R. coxata* + *R. brevitarsis* + *R. aurifera* + *R. scutellata*). The first group is defined by five synapomorphies (the slightly projected antennal insertion, the very high width of the gena, the color of the frontal triangle not contrasting with the ground color, the long frontal triangle, and a thin ceral plate) and the second one by three (presence of few and weak setulae on the frontoorbital plate, the brown and yellow knob, and sternite 5 arms medium in width).

**Biogeographic analysis.**—The biogeographical patterns of distribution of Muscidae are scarcely known in the world. For the Neotropical Region, only Hennig (1965) and more recently Carvalho (1999) analyzed patterns of distribution of Muscidae species in South America with a dispersalist and a cladistic view, respectively; however, in the southern part of this continent, below 30°S latitude but including the Andean highland northern of this latitude (Kuschel 1969, Cabrera and Willink 1973, Crisci et al. 1991, Morrone 1993, Morrone et al. 1994, Morrone and Lopretto 1994,

Amorim and Pires 1996), there are no historical biogeographic studies with Muscidae.

The biogeographical patterns of some endemic taxa in southern South America have been recently studied with cladistic biogeographic methods (Crisci et al. 1991; Morrone 1993, 1994; Morrone et al. 1994, 1997). Selected biological area cladograms proposed for southern South America are shown in Fig. 3.

The taxon-area cladograms of *Apsil* (Fig. 4) and *Reynoldsia* (Fig. 5) were compared with those patterns found (Fig. 3) and shown to be congruent with those biogeographic reconstructions.

The distribution pattern of *Apsil* species is more restricted than *Reynoldsia* species. *Apsil atripes* is the only species (Fig. 4) exclusively occurring to the north of the subantarctic area corresponding broadly to the Curicó area of central Chile of Morrone et al. (1997). They tried to explained the patterns of central Chile and their study supports a vicariant explanation of the patterns analyzed.

All *Reynoldsia* species are spread in the

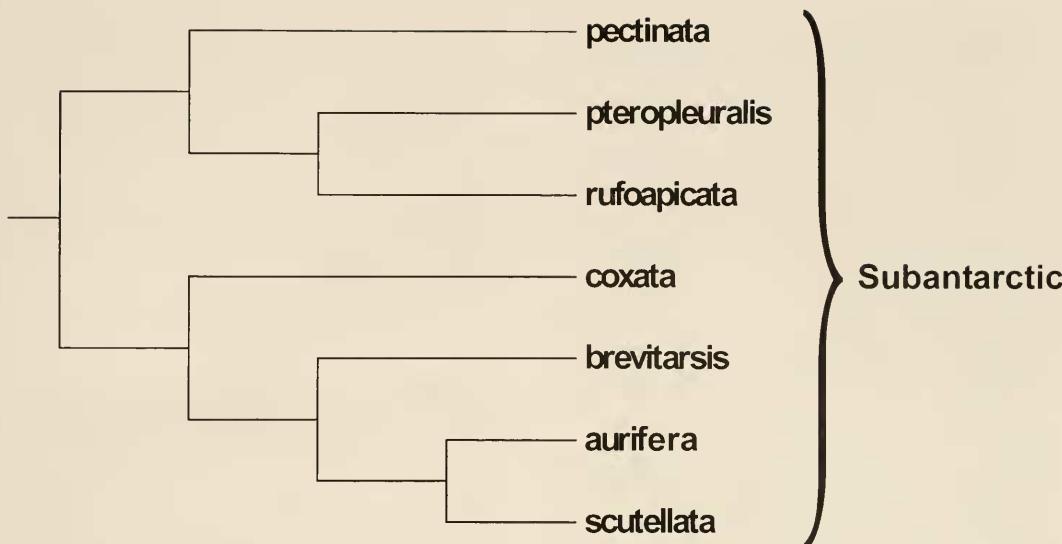


Fig. 5. Taxon-area cladogram of species of *Reynoldsia*.

subantarctic area, with only *Reynoldsia pectinata* occurring in Tierra del Fuego (Appendix 2). By the distribution pattern found in *Reynoldsia*, compared with the biological reconstruction of southern Chile by Morrone et al. 1994 (Fig. 3b), it could be expected that undescribed species of *Reynoldsia* occur in Malvinas Islands, which are part of the subantarctic area, here understood as a major monophyletic area (see Amorim and Pires 1996).

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## APPENDIX 1

Localities of species of *Apsil* in South America including latitude and longitude. Abbreviations: E = East, m = meters, k = kilometers, v. valley.

*Apsil apicata* Malloch 1934.—ARGENTINA: Lake Correntoso (40°44'S, 71°40'W); San Carlos de Bariloche (41°11'S, 71°23'W). CHILE: Casa Pangue (41°03'S, 71°52'W).

*Apsil atripes* Malloch 1934.—CHILE: Rio Colorado (33°04'S, 71°39'W); Curicó (34°59'S, 71°14'W); Talca, 800 m (35°20'S, 71°46'W); Concepción (San Rosendo) (37°16'S, 72°43'W).

*Apsil biseta* Malloch 1934.—ARGENTINA: Volcán (36°26'S, 67°09'W); San Carlos de Bariloche (41°11'S, 71°23'W). CHILE: Las Cabras, 1480 m (34°18'S, 71°19'W); Angol (37°47'S, 72°45'W); Malalcahuuelo (4–14 k E., 1080–1570 m.) (38°27'S, 71°35'W); Curacautín (38°28'S, 71°52'W); Villarica, 1250 m (39°15'S, 72°30'W); Coihaique (v. of Simpson river) (45°35'S, 72°08'W).

*Apsil dilata* Malloch 1934.—ARGENTINA: San Carlos de Bariloche (41°11'S, 71°23'W). CHILE: Ancud (41°53'S, 73°50'W); Punta (42°07'S, 73°49W); Castro (42°30'S, 73°46'W).

*Apsil maculipennis* Malloch 1934.—ARGENTINA: Volcán (36°26'S, 67°09'W); Lake Correntoso (40°44'S, 71°40'W); Puerto Blest (41°02'S, 71°59'W). CHILE: Malalcahuuelo (12 k E, 1080 m) (38°27'S, 71°35'W); Curacautín (38°28'S, 71°52'W); Villarica (39°15'S, 72°30'W); Osorno (40°35'S, 73°14'W); Parque Nacional Puyehue (40°40'S, 72°37'W); Coihaique (v. of Simpson river) (45°35'S, 72°08'W).

*Apsil maculiventris* Malloch 1929.—CHILE: Perales (36°40'S, 72°39'W).

*Apsil pennata* Malloch 1934.—ARGENTINA: San Carlos de Bariloche (41°11'S, 71°23'W). CHILE: Casa Pangue (41°03'S, 71°52'W).

*Apsil spatulata* Malloch 1934.—ARGENTINA: San Carlos de Bariloche (41°11'S, 71°23'W). CHILE: Peulla (41°06'S, 72°02'W); Puntra (42°07'S, 73°49'W).

#### APPENDIX 2

Localities of species of *Reynoldsia* in South America including latitude and longitude. Abbreviation: m = meters.

*Reynoldsia aurifera* Bigot 1885.—ARGENTINA: Lolog (40°05'S, 71°19'W). CHILE: Casa Pangue (41°03'S, 71°52'W); Aneud (41°53'S, 73°50'W).

*Reynoldsia brevitarsis* Malloch 1934.—ARGENTINA: San Carlos de Bariloche (4°11'S, 71°23'W); Lake Gutierrez (41°11'S, 72°23'W).

*Reynoldsia coxata* Malloch 1934.—ARGENTINA: Lolog (40°05'S, 71°19'W); San Carlos de Bariloche (41°11'S, 72°23'W).

*Reynoldsia pectinata* Malloch 1934.—ARGENTINA: Rio Grande (53°47'S, 67°42'W); Estancia Viamonte (54°02'S, 67°22'W). CHILE: Punta Arenas (53°09'S, 70°55'W).

*Reynoldsia pteropleuralis* Malloch 1934.—ARGENTINA: San Martín de los Andes (40°10'S, 71°21'W); Nahuel Huapi (41°03'S, 71°12'W); CHILE: Perales (36°40'S, 72°39'W).

*Reynoldsia rifoapicata* Malloch 1934.—ARGENTINA: San Martín de los Andes, 1500 m (40°10'S, 71°21'W); Lake Correntoso (40°44'S, 71°40'W); San Carlos de Bariloche (41°11'S, 71°23'W); Puerto Blest (41°02'S, 71°50'W).

*Reynoldsia scutellata* Malloch 1934.—CHILE: Angol (37°47'S, 72°45'W); Cerro Nahuelbuta, 650 m (37°48'S, 73°04'W); Galvarino (38°24'S, 72°47'W).